eggs, rather than appearing to be the odd one out in the clutch. However, brown-headed cowbirds seem not to vary much in their egg coloration and there is little evidence for egg mimicry. The cowbird chicks usually do not evict the host young from the nest but instead compete vigorously with them. In smaller host species, the young will often die of starvation, whereas in larger hosts all chicks can sometimes fledge. Unlike in the common cuckoo, which benefits from evicting the host nestlings to reduce competition, brown-headed cowbirds seem to benefit by keeping the host young in the nest because this maintains high provisioning by the parents. Because the parasitic chick is larger, it is still able to monopolise the food and to obtain a higher proportion of it than the host chicks.

The other four parasitic cowbird species are found principally in Central and South America. They vary in terms of host use, from the shiny cowbird (*M. bonariensis*), which utilises many host species, to the screaming cowbird (*M. rufoaxillaris*), which generally specialises on just one. Like the brown-headed cowbird, rates of parasitism by shiny cowbirds vary greatly and can be very high. In contrast to the brown-headed cowbird, the eggs of shiny cowbirds vary substantially in terms of colour and pattern. However, many of their hosts do not reject foreign eggs, and shiny cowbirds often do not seem to show obvious specialisation towards particular hosts. The reasons for such high egg variation are unclear. Recent work in Argentina shows that screaming cowbird fledglings have plumage colours and begging calls that are more similar to their primary hosts (baywing cowbirds, *Agelaioides badius*; a non-parasite) than are non-mimetic shiny cowbird young. Experiments putting either screaming or shiny cowbird young in baywing nests show high mortality of shiny cowbirds but little mortality of screaming cowbirds. This suggests that hosts reject parasitic young shortly after fledging by stopping feeding non-mimetic fledglings, which subsequently die. The conundrum here is why hosts wait until the fledgling stage to reject foreign chicks, by which time they have already invested a great deal of time and energy.

Our knowledge of the diversity brood parasites and their hosts, in particular their breeding adaptations, has substantially improved in recent years, in part through study of a greater range of species. The more we study brood parasites, the more we have to learn and the greater the range of their adaptions we find. Exciting questions remain, including whether chick mimicry exists other systems, why such differences in evolutionary trajectories and adaptations have occurred among species, and what other deceptive traits parasites have that we have yet to discover. We know very little about the various species of brood parasite that live in under-studied parts of the world, especially areas of east and southeast Asia and New Guinea, so stay tuned for more surprises.

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Centre for Ecology and Conservation, University of Exeter, Cornwall Campus, Penryn, TR10 9EZ, UK.
E-mail: martin.stevens@exeter.ac.uk

Correspondences

A new galloping gait in an insect

Jochen Smolka[1,*], Marcus J. Byrne[2], Clarke H. Scholtz[3], and Marie Dacke[1,2]

An estimated three million insect species all walk using variations of the alternating tripod gait [1]. At any one time, these animals hold one stable triangle of legs steady while swinging the opposite triangle forward. Here, we report the discovery that three different flightless desert dung beetles use an additional gallop-like gait, which has never been described in any insect before. Like a bounding hare, the beetles propel their body forward by synchronously stepping with both middle legs and then both front legs. Surprisingly, this peculiar galloping gait delivers lower speeds than the alternating tripod gait. Why these beetles have shifted so radically away from the most widely used walking style on our planet is as yet unknown.

Like all insects described so far, four of seven observed species of *Pachysoma*, a dung beetle genus endemic to the coastal deserts of South Africa and Namibia, typically walk with an alternating tripod gait (Supplemental information). In this gait, the first and third leg on one side of the body move in unison with the contralateral middle leg [2] (Figure 1A,C), forming a moving tripod. This tripod alternates with the static, stable tripod made up of the remaining three legs. In many insects, this pattern of leg coordination changes with speed, creating a continuum of stepping patterns ranging from the tripod gait to a 'tetrapod gait', where only two legs (diagonally opposed, one on either side) swing at any one time [3–5]. All of these seemingly diverse patterns, however, follow a small set of simple rules [2], including the principal rule that each leg moves out of phase with its contralateral pair, i.e. legs of a pair move alternately. In almost all insect species, synchronous (in-phase) stepping of a leg pair is only observed in exceptional

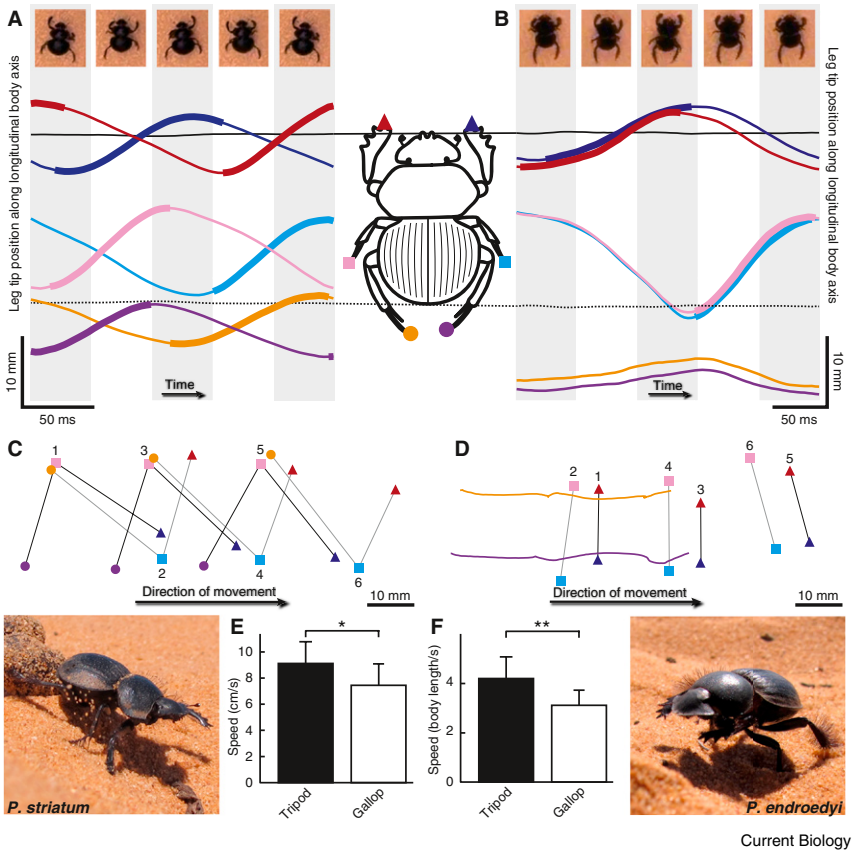

Figure 1. Comparison of tripod gait and gallop.
(A,B) Movement of legs relative to the beetle's body during an average step cycle. *P. striatum* (bottom left) walks in the insect-typical tripod gait; legs of each pair step alternately (A). *P. endroedyi* (bottom right) employs a galloping gait; legs of a pair move in unison (B). Images at the top are video frames at the respective times during the stride. Individual legs are colour-coded as indicated on the schematic beetle. Thin lines indicate periods of ground contact, thick lines striding periods. In the galloping gait, hind legs are dragged behind (thin lines). Position of front of head and rear of abdomen are indicated by solid and dotted black lines, respectively. Note the different time scales. (C,D) Bird's-eye view of footsteps created by three typical step cycles in *P. striatum* (C) and *P. endroedyi* (D). Legs are colour-coded as above, thin lines connect legs that move together (black/grey lines represent first/second half of step cycle, respectively). Numbers indicate the order of footfalls. (E,F) Average walking speed measured in tripod-walking *P. striatum* (black bars) and galloping *P. endroedyi* (white bars), shown as absolute values (E) and relative to body length (F). All bars show mean ± s.d. of ten beetles per species. Statistics were performed using independent-sample two-sided t-tests. * $p < 0.05$; ** $p < 0.01$.

circumstances, e.g. when crossing an obstacle [6], when swimming [7] or for a few steps when the animal begins to walk [4].

Three other species of *Pachysoma* — *P. endroedyi* (Figure 1, bottom right), *P. hippocrates* and *P. glentoni* — are the exception to this rule. Living on the sands of Namaqualand (South Africa), these flightless desert dung beetles forage on dry vertebrate dung and plant detritus, which they drag with their hind legs while walking forwards to their burrow [8]. Although they can walk in the normal tripod gait, these beetles usually employ a unique galloping gait, in which they move each pair of legs synchronously, stepping alternately with the front and the middle legs (Figure 1B,D; Supplemental information). The hind legs are dragged behind, even if the beetle carries no load, and seem to contribute little to propulsion. Although no aerial phase occurs, as is the case in galloping mammals, the leg coordination is that of a gallop, specifically a full bound as found in hares and rabbits [9].

There should be significant reasons for the evolution of this additional gait, which supplements the most common walking gait in the animal kingdom. In light of this, it is useful to consider the only other insect species walking with a similar, synchronous gait: the primitive jumping bristletail *Petrobius brevistylis* [10]. The bristletail's 'jumping gait' differs from the *Pachysoma* gallop in that all three leg pairs alternate in metachronal order — back, middle, front — and that the abdomen and tail are dragged on the ground for stability. Furthermore, a galloping *Pachysoma* can maintain this gait for at least 100 m, whereas on a rocky beach, the jumping gait of *Petrobius* will be restricted to decimetres at most. Mechanically, the jumping gait is enabled by the bristletails' leg morphology, in which the first and second joints (pleurites–coxa and coxa–trochanter, respectively) are unique among the arthropods, allowing extensive leg movements. *Petrobius* also has unusual thoracic and abdominal musculature, which is highly specialised for another type of locomotion: fast escape jump reactions [11]. This musculature enables the animals to cover up to twenty body lengths per second with their jumping gait, which is twice as fast as other, similarly small insects. We found no such speed advantage for the *Pachysoma* galloping gait. On the contrary, when observing beetles on sandpaper or fabric surfaces (to provide grip), we measured running speeds in the tripod-walking *P. striatum* that were slightly but significantly faster than those for the sympatric, similarly-sized galloping *P. endroedyi* (Figure 1F,G). This is true both in absolute terms (9.1 ± 1.5 cm/s vs. 7.6 ± 1.6 cm/s, mean ± s.d.; two-sample t-test, $t = -2.1$, $d.f. = 18$, $p = 0.0498$) and in relation to body size (4.2 ± 0.9 body lengths/s vs. 3.1 ± 0.6 body lengths/s, mean ± s.d.; two-sample t-test, $t = -3.2$, $d.f. = 18$, $p = 0.003$).

These results suggest that *Pachysoma*, in contrast to *Petrobius*, have not evolved their galloping gait to be faster. The reason why this strange and rare gait has evolved remains unknown. Does it provide an advantage in terms of energy consumption or mechanical stress? Does it make it easier to move straight or stabilise head and eyes while transporting large loads across shifting sands? If true, this would suggest an advantage for navigation between the nest and a foraging site. Testing these hypotheses will bring

us one step closer to understanding the ecological and evolutionary significance of *Pachysoma's* unusual gait.

Supplemental Information
Supplemental Information including experimental procedures and a movie can be found with this article online at http://dx.doi.org/10.1016/j.cub.2013.09.031.

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[1]Department of Biology, Lund University, 22362 Lund, Sweden. [2]School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Wits 2050, South Africa. [3]Department of Zoology and Entomology, University of Pretoria, Pretoria 0002; South Africa.
*E-mail: jochen.smolka@biol.lu.se

Badger social networks correlate with tuberculosis infection

Nicola Weber[1], Stephen P. Carter[2], Sasha R.X. Dall[1], Richard J. Delahay[2], Jennifer L. McDonald[1], Stuart Bearhop[1], and Robbie A. McDonald[3]

Although disease hosts are classically assumed to interact randomly [1], infection is likely to spread across structured and dynamic contact networks [2]. We used social network analyses to investigate contact patterns of group-living European badgers, *Meles meles*, which are an important wildlife reservoir of bovine tuberculosis (TB). We found that TB test-positive badgers were socially isolated from their own groups but were more important for flow, potentially of infection, between social groups. The distinctive social position of infected badgers may help explain how social stability mitigates, and social perturbation increases, the spread of infection in badgers.

Tuberculosis, caused by *Mycobacterium bovis*, is a zoonotic infection of cattle and is a global challenge in animal health. In the U.S.A., New Zealand, Spain, France, Ireland and Britain, TB control in cattle is complicated by reservoirs of infection in wildlife. In Britain, badgers are a major wildlife reservoir and although intensive, pro-active badger culling can reduce TB incidence in cattle in culled areas, it has also been associated with increases in prevalence in badgers and increases in incidence in cattle in adjacent areas [3,4]. Hence, reductions in badger density appear not to yield quantitatively equivalent reductions in TB transmission. Across much of the species' range, badgers live in territorial social groups that share dens, known as setts, and increases in TB transmission associated with culling have been hypothesised to arise from perturbation of these social structures [5]. Therefore, understanding badger social behaviour and its relationship to infection will help in developing effective TB control strategies.

We used proximity-logging radio tags to monitor patterns of sett use and to record remotely interactions among badgers in an intensively-studied, undisturbed, high-density population at Woodchester Park, Gloucestershire, England. We sampled eight social groups and tagged 51 adult and sub-adult badgers. 21 badgers (41%) tested positive on at least one occasion to at least one of two live-animal diagnostic tests for TB infection. We analysed within-group and among-group contacts separately and derived three measures of social network centrality: Degree (frequency and/or duration of immediate contacts of an individual), Closeness (distance of an individual to all others) and Flow-Betweenness (a measure of positional advantage in the 'flow', potentially of infection, across the network, specifically, the contribution of a given individual to all possible pathways connecting all pairs in the network).

We found statistically significant relationships between network position and TB test outcome (Figure 1). Within-group degree and closeness were lower for test-positive (TB+) than for test-negative (TB–) badgers in autumn and winter, but did not differ significantly in spring and summer; among-group degree and closeness did not differ significantly with respect to infection (see Table S1 in the Supplemental Information). Within-group flow-betweenness was significantly lower for TB+ badgers in autumn, whereas among-group flow-betweenness was significantly higher for TB+ badgers in summer and winter (Table S2). Social behaviour was related to spatial behaviour; time spent resting at outlying setts was negatively related to time spent with badgers from their own group but positively related to time spent with members of other social groups (Table S3).

From a fundamental perspective, we cannot infer causation of these patterns because experimental interventions in this system are ethically challenging. However, underlying mechanisms could operate as in other host–pathogen systems. Individuals occupying particular network positions may be intrinsically or behaviourally disposed to increased exposure or susceptibility to infection. Alternatively, infection may lead to an individual's occupancy of a particular